

COMPARATIVE ANATOMY OF THE LEAF-BEARING  
CACTACEAE, VI  
THE XYLEM OF PERESKIA SACHAROSA  
AND PERESKIA ACULEATA

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THE MOST PRIMITIVE living representatives of the Cactaceae have been considered to be *Pereskia sacharosa* Griseb. and *P. aculeata* Mill. Such a conclusion is based largely upon the claim that the flowers of these species have "superior" ovaries (Berger, 1926; Buxbaum, 1953). It is of interest to determine whether evidence from other parts of the plants supports such a phylogenetic generalization. Evidence from the xylem is considered in this paper. Additional evidence from other parts of the plants will be considered subsequently.

PERESKIA SACHAROSA

During its earlier stages of growth, this species is considered to be a shrub which ultimately may become a small tree eight meters high. As in the case of other wide-ranging putative species of *Pereskia*, plants from different localities exhibit more or less conspicuous differences in their leaves, general habit of growth, spination, and floral characters. At present, it is uncertain whether such differences are produced by different environmental influences or are due to genetic differences at racial or specific levels.

My anatomical specimens of this species have been obtained from the following sources: 1) From a wild plant collected by Carenzo and Legname in Jujuy Province, Argentina; 2) from a wild plant collected by Cárdenas in the Department of Cochabamba, Bolivia; 3) from a plant growing in the Missouri Botanical Garden; and 4) from a plant growing at the New York Botanical Garden. The ranges of variability in the xylem of the four plants are so closely similar as to provide no reliable anatomical criteria for differentiating one plant from the others.

In the outer secondary xylem of larger stems the vessels occur singly and in small clusters (Figs. 1, 3), but tend at times in their overall arrangement to exhibit more or less conspicuous concentric patterns (Fig. 1). The wood parenchyma is scanty paratracheal (Fig. 3), having lignified walls. The multiseriate rays are composed of cells of varying size, form, and orientation which likewise have comparatively thick lignified walls

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(FIGS. 3, 5). Where crystals of calcium oxalate are present in ray cells they occur singly or as several independent ones, druses being absent. The distribution of vessels and wood parenchyma in comparable secondary xylem of roots is similar (FIG. 2) but the multiseriate rays are broader (FIGS. 2, 6). The rays, as in those of the stem, may be composed, throughout their radial extension, of cells with lignified walls. In some cases, however, the first-formed multiseriate rays in the center of the root are composed at first of cells having thin, unlignified walls. These cells differ from subsequently formed lignified ones in containing isotropic granular contents, rather than starch.

It is evident that the secondary xylem in stems and roots of *Pereskia sacharosa* is of a phylogenetically highly evolved structure such as occurs in trees and shrubs of normal form in a number of other dicotyledonous families. For a discussion of pitting, perforation plates, and other structures visible under higher magnification, the reader is referred to the fourth paper of this series (Bailey & Srivastava, 1962).

There are certain ontogenetic changes in rays that should be considered in dealing with the secondary xylem of the leaf-bearing Cactaceae. The multiseriate rays of dicotyledons commonly exhibit significant changes in passing from the first-formed to the later-formed secondary xylem (Chattaway, 1933; Barghoorn, 1940, 1941a). The first-formed part of multiseriate rays adjacent to gaps in the primary body (particularly of stems having elongated internodes) frequently tend to be narrow and vertically extensive as seen in tangential longitudinal sections (FIG. 8). During subsequent radial extension of such rays they tend to become wider and dissected sooner or later into vertically less extensive parts which ultimately may assume fusiform outlines (FIG. 6). Of the various cytological changes involved in the modification of such rays the transformation of ray initials into fusiform cambial initials is particularly significant. Furthermore, the dissected parts of the original rays tend to be laterally displaced during increase in girth of the cambium. In addition, the cells of the rays generally vary more or less in form and orientation during successive modifications of the multiseriate rays, the cells in the first-formed part of the rays tending to have a longer vertical axis (i.e., being "erect"), whereas in subsequently formed parts of the rays they become more or less isodiametric or even radially extensive (i.e., "procumbent"). Such changes in multiseriate rays vary in degree, and may be precocious and relatively abrupt, gradual, or considerably delayed, varying at least in part with different rates of growth and the enlargement of stems.

In roots of *Pereskia sacharosa*, the first-formed multiseriate rays broaden conspicuously during their radial extension outward (FIG. 2). In their first-formed part they are not only much narrower, but also more extensive vertically. During their radial extension outward they tend to become dissected into lower derivatives which assume fusiform outlines as seen in tangential longitudinal sections (FIG. 6). In stems from some parts of a mature plant, the first-formed parts of the rays are narrower and more extensive vertically, but subsequent widening and dissection of

the rays is much less conspicuous than in roots (compare FIGS. 1 and 2, 5 and 6). In other stems from the same plant, the first-formed rays of the secondary xylem are broader, subsequently becoming narrower (FIG. 4) and then broadening somewhat in the later-formed xylem (FIG. 3).

Such variations in the form of the multiseriate rays appear to be correlated with differences in the development of the primary body. The diameter of the primary vascular cylinder and pith commonly varies in different stems of the same plant from three millimeters to one centimeter. As seen in transverse sections, the two extreme forms of eusteles may be composed of the same number of fascicular and interfascicular parts. Although there is some variation in the breadth of fascicular parts, the conspicuous differences in circumference of the eusteles appears to be due largely to differences in the width of interfascicular parts (i.e., parenchymatous gaps). In the case of the smaller young stems, cambial activity develops precociously in the parenchyma of the narrow gaps, and the multiseriate rays of the secondary xylem are relatively narrow when first formed. On the contrary, in the larger young stems the parenchymatous gaps tend to widen by division and transverse expansion of their constituent cells for a considerable time after cambial activity is initiated in the fascicular parts of the eustele (FIG. 4). It should be noted in this connection that the widening of the interfascicular parts and the delayed initiation of cambial activity within them leads, not only to a conspicuous increase in the circumference of the eustele, but also permits a marked increase in the diameter of the pith. Furthermore, when multiseriate rays of the secondary body are initiated they tend at first to be considerably broader than in the case of smaller stems (FIG. 4).

In both stems and roots of *Pereskia sacharosa*, the parenchymatous cells of the first-formed part of the multiseriate rays are of "erect" form but are shorter than the fusiform initials of the cambium. Subsequent changes in the size, form, and orientation of the ray cells, as seen in radial longitudinal sections of the xylem, are precocious and abrupt. Most of the cells become more or less isodiametric, except on the sides of the rays and their upper and lower margins where they may retain an erect form. In addition, some radial tiers of slender cells of procumbent orientation tend to occur within the rays.

#### PERESKIA ACULEATA

This species is widely distributed in the West Indies and in eastern and northern South America. Because of the edibility of its fruits and leaves, its ornamental value in gardens, and its use in hedges, its original range has been considerably extended by man. It is therefore difficult at times to determine with certainty whether plants now growing in the wild (e.g., Florida or Mexico) are native or were introduced and escaped from cultivation.

The species is commonly described as a shrub, frequently producing long clambering branches and forming vines three to ten meters long

(cf. Britton & Rose, 1919). The larger, older stems may have a diameter of two to three centimeters with a primary vascular cylinder and pith five to six millimeters in diameter. The ultimate terminal branches of mature plants are, in general, more numerous and more slender than those of *Pereskia sacharosa*, grading down in many cases to as little as two millimeters in diameter with correspondingly slender primary vascular cylinders and pith. Furthermore, in branches of comparable diameter, the eusteles of *P. aculeata* are composed of fewer fascicular strands and comparatively broader parenchymatous gaps. This conspicuous difference in the primary bodies of the two species appears to be correlated with the tendency of *P. aculeata* to have two-trace unilacunar nodes, whereas *P. sacharosa* commonly has four to six vascular strands at its unilacunar nodes. (For illustrations see Bailey, 1960.)

The young branches of *Pereskia aculeata* are commonly of two different forms: slender woody ones and broader, very succulent ones, referred to in Boke's (1954) developmental investigations as long shoots and spur shoots respectively. In the former stems cambial activity and the formation of secondary xylem are precocious, whereas in the latter stems the formation of secondary xylem is delayed and the thickness of the pith and cortex is relatively greater. At times, the most slender woody stems bear short, broad, highly succulent laterals. In such cases the slender woody stems have long internodes, whereas the succulent laterals have short internodes. These abrupt differences in external form and internal structure resemble those between long shoots (pycnoxylic<sup>2</sup>) and short shoots (manoxylic<sup>2</sup>) that occur in *Ginkgo biloba* L. (Gunckel & Wetmore, 1946a, 1946b) in *Cercidiphyllum japonicum* Sieb. & Zucc. (Titman & Wetmore 1955), and a number of other plants.

The structure of the secondary xylem of *Pereskia aculeata* varies markedly in different parts of a mature plant. As so frequently happens in scandent representatives of other dicotyledonous families, e.g., Hippocrateaceae, Icacinaceae, Schisandraceae, etc., many stems exhibit more or less abrupt transitions from first-formed, denser, more nearly normal secondary xylem to phylogenetically highly modified, softer, more porous forms of tissue. The denser, earlier-formed secondary xylem (illustrated in FIG. 7) resembles the secondary xylem of *P. sacharosa* (FIG. 7). The vessels, allowing for higher magnification, are of comparable size, form, and distribution. The wood parenchyma is scanty paratracheal and has strongly lignified walls. The multiseriate rays, although somewhat narrower than those of *P. sacharosa*, have thick, strongly lignified cell walls. On the contrary, the later-formed secondary xylem has much enlarged vessels, as well as radial rows of much smaller ones. In addition to scanty wood parenchyma about vessels in the denser parts, it has arcs or concentric zones of unlignified parenchyma. The cells of the broadened rays (compare FIGS. 2 and 3) are very thin, unlignified, and many of them contain druses (FIG. 16). Furthermore, the number of thick-walled libriform fibers is greatly reduced.

<sup>2</sup> Using these terms as redefined by Titman and Wetmore.

In other stems, even from the same plant, the transition from normal dense to modified secondary xylem occurs at varying distances from the pith. The transition to xylem containing huge vessels may be abrupt or gradual (FIG. 11). Furthermore, the volume and distributional patterns of the unignified<sup>3</sup> parenchyma varies markedly from stem to stem. In the xylem illustrated in FIG. 10, the unignified parenchyma occurs in broad concentricities alternating with zones of strongly lignified tissue. The relatively narrow multiseriate rays, unlike those of FIG. 7, have lignified walls, except where they pass radially through the broad zones of unignified parenchyma. In contrast to this, the outer secondary xylem in FIG. 11, although exhibiting a conspicuous enlargement of vessels has unignified parenchyma that is confined to narrow arcs and concentricities.

The roots of *Pereskia aculeata* superficially resemble those of *P. sacharosa*, having numerous rapidly broadening multiseriate rays (compare FIGS. 2 and 14), but the ray cells of *P. aculeata*, many of which contain druses of calcium oxalate, differ in having thin, unignified walls (FIG. 14). It should be noted in this connection that the first-formed ray cells in the center of some roots of *P. sacharosa*, although having thin unignified walls, contain no druses and little if any starch. Furthermore, in roots, as in stems (FIGS. 8, 9), of *P. aculeata*, the multiseriate rays tend to remain vertically extensive, and in passing radially outward do not exhibit precocious and conspicuous dissection into laterally displaced parts as illustrated for *P. sacharosa* in FIG. 6. The unignified rays of both roots and stems of *P. aculeata*, not only contain abundant druses (FIG. 16) but also at times varying numbers of mucilage cells (FIG. 17).

In many stems of *Pereskia aculeata*, owing to the breadth of the parenchymatous gaps in the eustele, the multiseriate rays tend to be broader when first formed than in the subsequently formed secondary xylem. As indicated in FIG. 11, this reduction in ray width resembles that which occurs in very stout young stems of *P. sacharosa* (FIG. 4). However, in the case of *P. aculeata*, the cells of the first-formed ray tissue tend to resemble fusiform cambial initials in their vertical extension (FIG. 12). In other words, the first-formed ray initials of the cambium resemble fusiform initials in size and orientation. Subsequent transverse divisions of the ray initials lead to the formation of less "erect" ray cells (FIG. 13) and ultimately to more or less isodiametric or somewhat procumbent ones. It should be noted in this connection that similarities between ray initials and fusiform initials occur in the first-formed cambium of some other dicotyledonous families (Barghoorn, 1941).

Tyloses are of sporadic occurrence in the vessels of *Pereskia aculeata*. In some stems, they are not only abundant but contain starch (FIG. 15).

<sup>3</sup>The unignified primary walls of leaf-bearing Cactaceae give a red coloration in sections stained with Haidenhain's haematoxylin and safranin. Therefore, in testing for lignification it is advisable to use the phloroglucin-HCl and Mäule reactions where unignified walls remain colorless, as in FIGS. 10 and 14.

## DISCUSSION

In the fourth paper of this series (Bailey & Srivastava, 1962) we discussed the finer structural details in derivatives of the fusiform initials of the cambium. We found that the ranges of variability of potential diagnostic criteria in the leaf-bearing genera *Pereskia*, *Pereskiopsis*, and *Quiabentia* are extensive, not only in different collections of the same taxon and in the same clone grown under different environmental influences, but also in different parts of the same mature plant. It is evident that the grosser anatomical features of *Pereskia aculeata* (e.g., size and distribution of vessels, abundance, distributional patterns, and internal structure of wood parenchyma, and the size, form and internal structure of the multiseriate rays) likewise vary markedly even in different parts of a single plant.

Anatomical surveys of the dicotyledons as a whole demonstrate that the xylem of vines and lianas commonly exhibits trends of highly advanced phylogenetic modification, i.e., in comparisons with the structure of related trees and large woody shrubs of the same genus, family, or order. This obviously occurs in *Pereskia aculeata* in contrast to *P. sacharosa*. Thus, although *P. sacharosa* may have retained a form of xylem characteristic of ancestral leaf-bearing cacti, the internal structure of stems and roots of *P. aculeata* negates any possibility of considering this species to be the most primitive living representative of the Cactaceae. Therefore, in searching for such a primitive representative, it will be of interest in succeeding papers of this series to compare the internal structure of *P. sacharosa* with that of other arborescent and woody, shrubby species of *Pereskia*.

The tendencies in the xylem of *Pereskia aculeata* toward the formation of parenchymatous cells having thin, un lignified walls, with concomitant inclusions of druses, are extensively developed in roots of Andean pereskias and in stems of *Pereskiopsis* and *Quiabentia*. They seem to be correlated in some manner with increasing succulence and merit detailed investigation. Furthermore, the tendency in some stems of both *P. sacharosa* and *P. aculeata* toward increase in circumference of the primary vascular cylinder and in diameter of the pith after cambial activity is initiated in the fascicular parts of the stele is a phenomenon which becomes greatly exaggerated in many representatives of the Cactaceae. It is a conspicuous feature in dealing with the larger basal stems of pereskias from Southern Mexico and Central America and in stems of certain species of *Pereskiopsis* and *Quiabentia*.

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## EXPLANATION OF PLATES

### PLATE I

FIGS. 1-3. Transverse sections of the secondary xylem of *Pereskia sacharosa*. 1, Outer xylem from stem 7 cm. in diameter,  $\times 11$ . 2, Xylem from root 3 cm. in diameter,  $\times 11$ . 3, Xylem of FIG. 1 more highly magnified,  $\times 88$ .

### PLATE II

FIGS. 4-6. Transverse and tangential longitudinal sections of *Pereskia sacharosa* showing structure of multiseriate rays. 4, Transverse section of inner xylem from a stem 7 cm. in diameter,  $\times 34$ . 5, Tangential section from outermost xylem of FIG. 1,  $\times 43$ . 6, Tangential section of outermost xylem of FIG. 2,  $\times 43$ .

### PLATE III

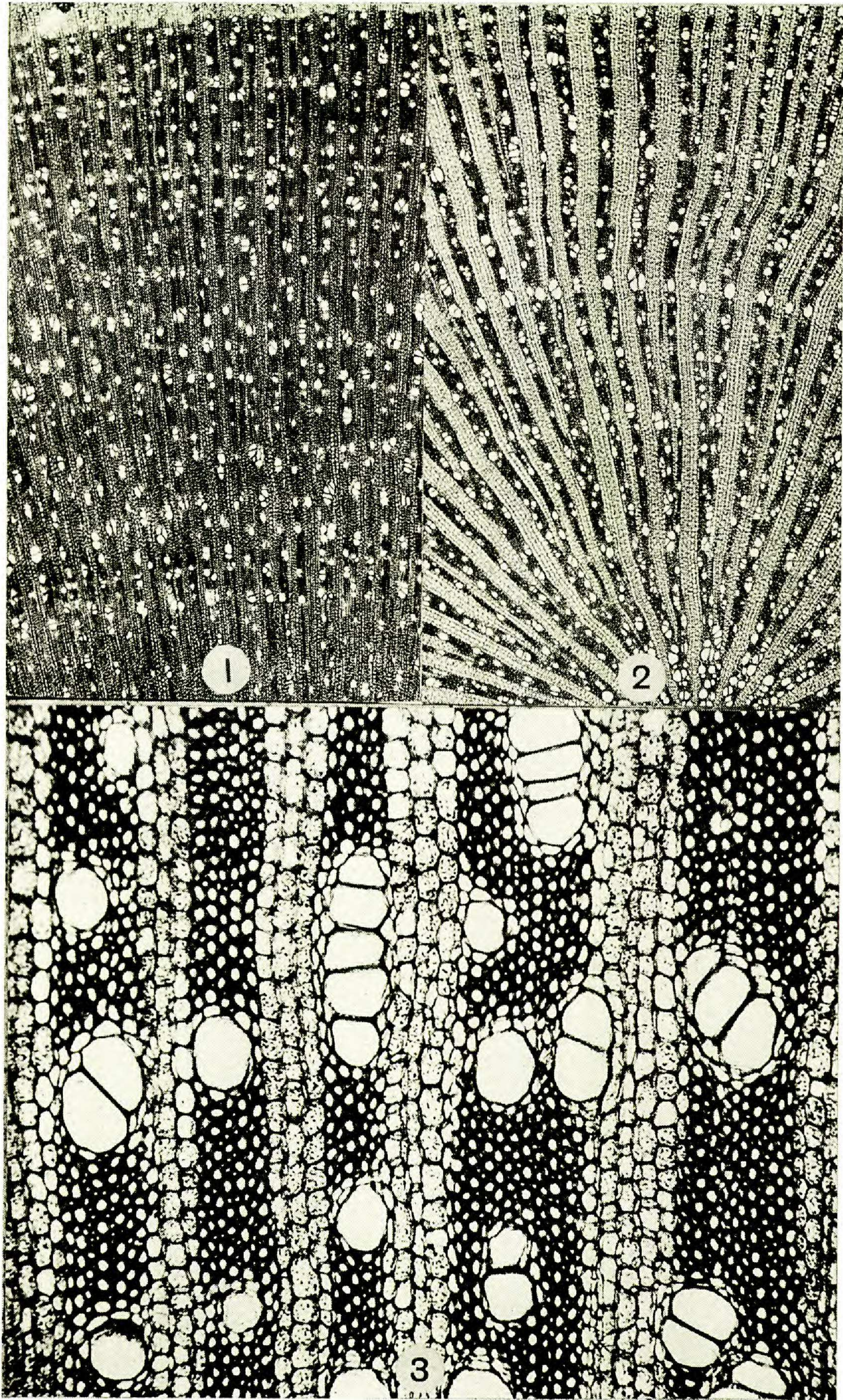
FIGS. 7-9. Transverse and tangential longitudinal sections of *Pereskia aculeata* from stem 2.5 cm. in diameter. 7, Transverse section of xylem,  $\times 34$ . 8, Tangential section of denser xylem,  $\times 43$ . 9, Tangential section of outer, softer xylem,  $\times 43$ .

### PLATE IV

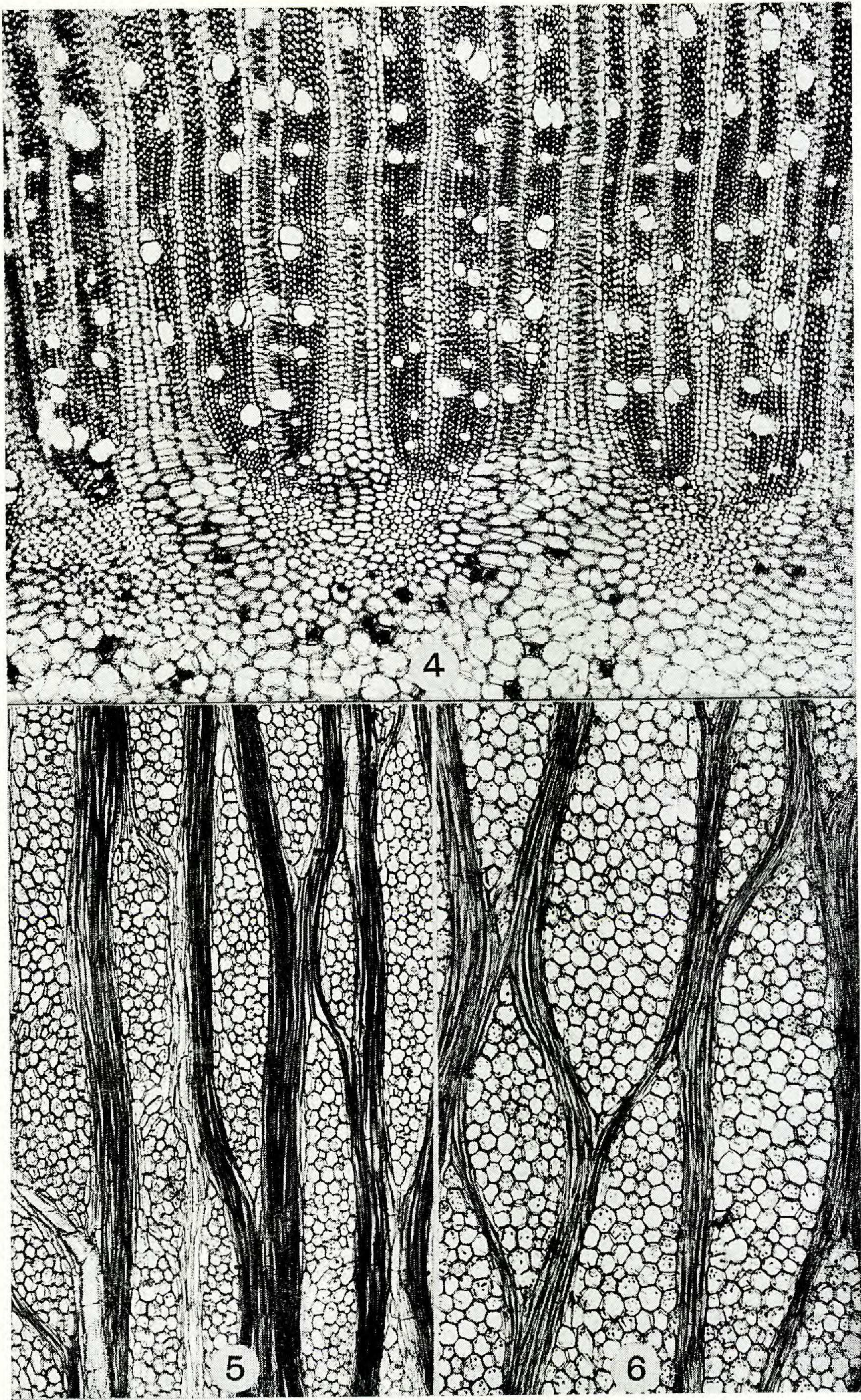
FIGS. 10-13. Transverse and longitudinal sections of the xylem from stems of *Pereskia aculeata*. 10, Transverse section treated with phloroglucin-HCl, showing concentric zones of unligified parenchyma (white),  $\times 34$ . 11, Transverse section of inner xylem, showing changes in ray structure and narrow arcs of thin-walled wood parenchyma,  $\times 43$ . 12, Tangential section of first-formed secondary xylem,  $\times 88$ . 13, Radial section showing transitional changes in the height of ray cells,  $\times 88$ .

## PLATE V

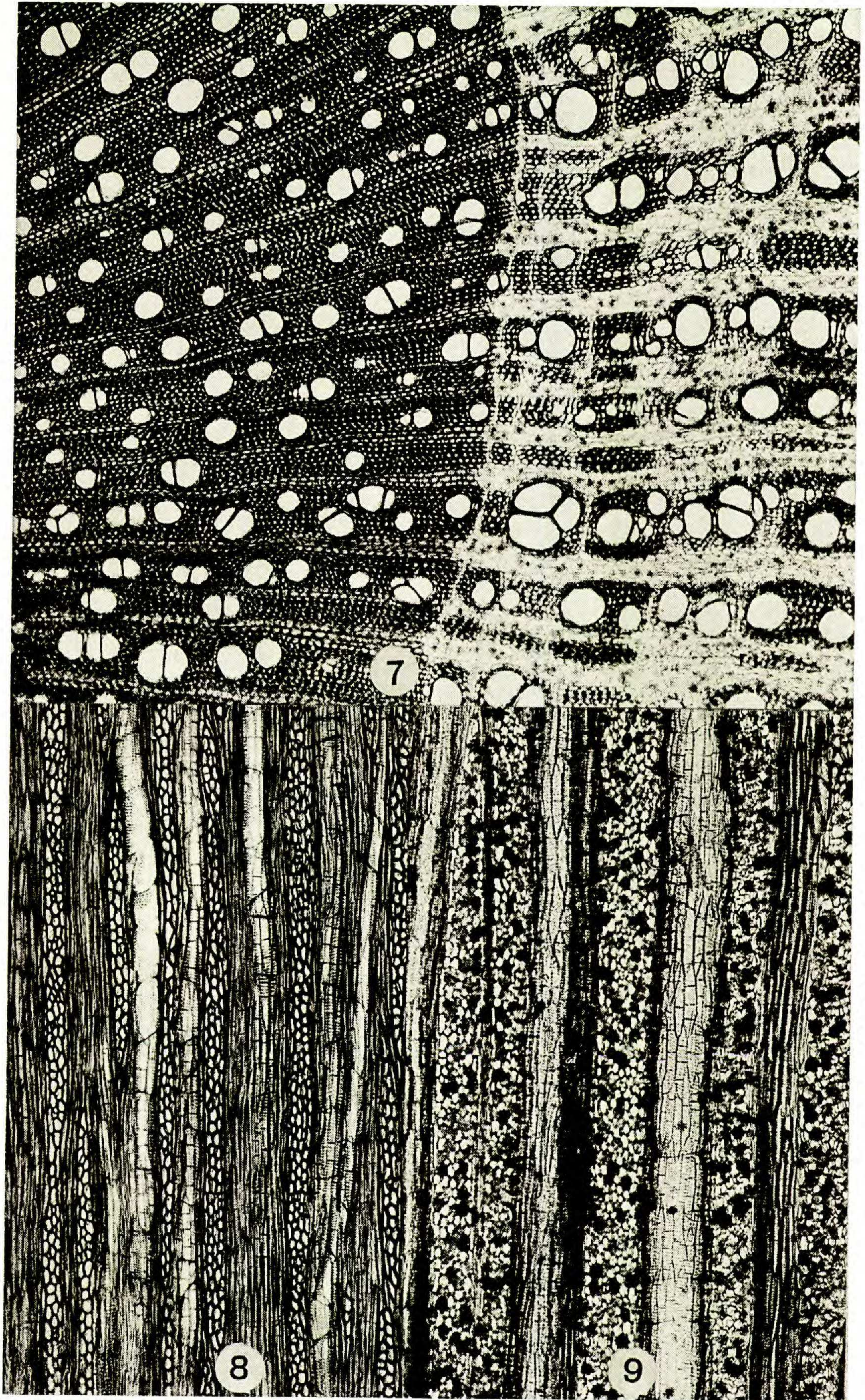
FIGS. 14-17. Transverse and tangential longitudinal sections of *Pereskia aculeata*. 14, Transverse section of root, treated with phloroglucin-HCl, showing unligified multiseriate rays (white),  $\times 34$ . 15, Transverse section of vessel, showing starch in tyloses,  $\times 107$ . 16, Part of FIG. 9, more highly magnified, showing druses in multiseriate ray,  $\times 107$ . 17, Tangential section of xylem, showing mucilage cells (arrows) in multiseriate ray,  $\times 107$ .



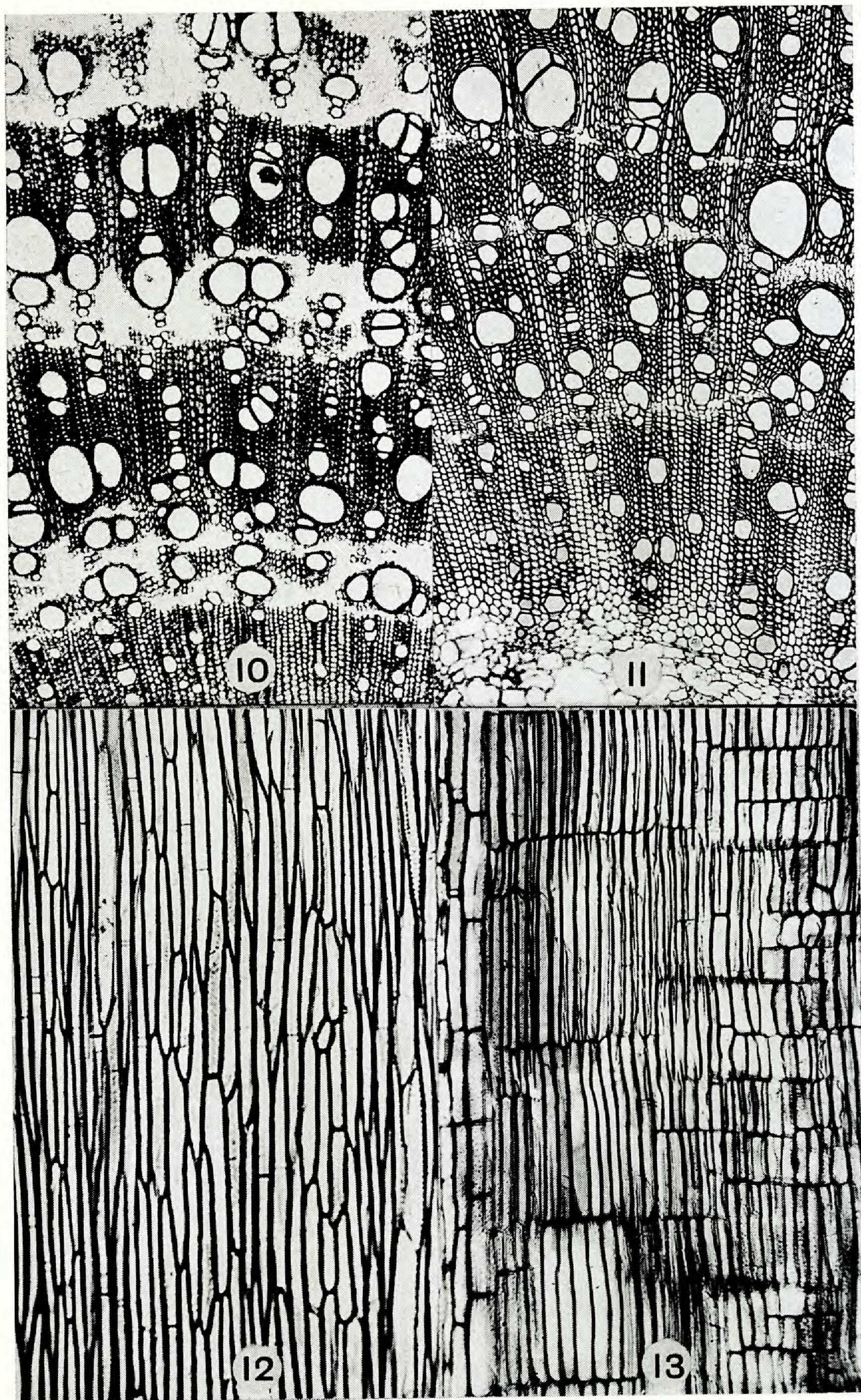
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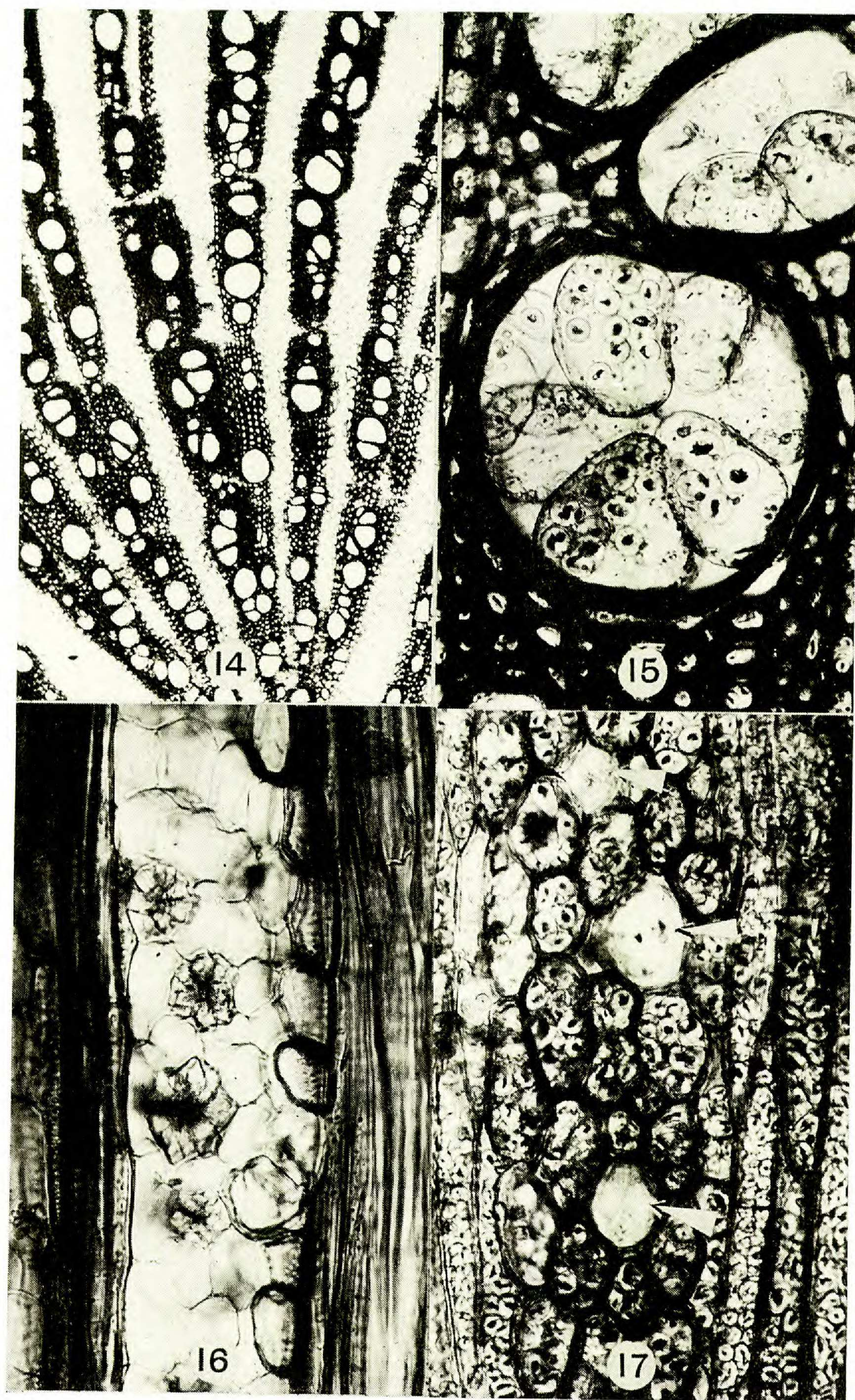
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